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Dependence of canopy light distribution on leaf and canopy structure for two cotton (*Gossypium*) species

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Abstract

The light environment within a crop canopy is an important determinant of the potential photosynthetic activity of the crop. The photon flux environment within the crop is influenced by the total incoming radiation and the structure of the plant canopy. In this study, the light environment within two economically important species of cotton (*Gossypium*, sps.) that show diverse growth habits was examined at different growth stages. *G. hirsutum* had very regular leaf shapes throughout the growing season, and was diaheliotropic. *G. barbadense* had large, fairly flat leaves early in the season that progressively became more cupped at increasing mainstem positions, and had no heliotropic response. These differences in leaf shapes and solar tracking altered the leaf and canopy light environment. Estimated total diurnal light intercepted by upper canopy leaves was found to be lower for *G. barbadense* than for *G. hirsutum*, due in part to the cupping of the leaf surface. Alternatively, the cupping of the *G. barbadense* leaves resulted in a more erectophile canopy, increasing PFD to lower canopy leaves in the *G. barbadense* canopy particularly later in the season relative to that PFD observed in the *G. hirsutum* canopy. This redistribution of light to lower canopy leaves has been suggested to be beneficial by increasing net canopy photosynthesis. The cupping of the *G. barbadense* leaves, in addition to distributing light over a greater photosynthetically active area, may be beneficial by reducing photoinhibition. Additionally, the extreme cupping of the *G. barbadense* leaves results in illumination of the abaxial surface during portions of the day, which may further increase the photosynthetically active area and contribute to total canopy carbon uptake.

1. Introduction

The light environment within a canopy is important for determining the potential carbon uptake by the crop. The potential carbon uptake depends not only on the amount

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of total photosynthetically active radiation (PAR) intercepted, but also on the distribution of the photon flux within the crop canopy. The total PAR intercepted is a function of the leaf area index of the crop (Heitholt et al., 1992; Heitholt, 1994). The PAR distribution within the canopy depends on the canopy architecture, which in turn is determined by the position and orientation of the foliage within the canopy.

Previous work has examined the interaction between canopy architecture of row crops and light profile within the canopy, and the consequent impact of photon flux profile on photosynthesis (reviewed by Monsi et al., 1973; Lemeur and Blad, 1974). Studies have suggested that a more even distribution of photon flux density (PFD) within a canopy by increased PAR penetration to lower layers can enhance photosynthesis (Kuroiwa, 1970; Aikman, 1989; Herbert, 1991). In particular, a more erect distribution of upper foliage elements decreased PAR interception by upper layers, and increased light penetration to lower leaves (Herbert, 1991; Herbert, 1992). This redistribution of light to lower layers resulted in a greater total carbon uptake due to enhanced photosynthetic activity of lower leaves (Kuroiwa, 1970; Constable, 1986; Wells et al., 1986).

The two most economically important species of cotton (*Gossypium hirsutum* and *G. barbadense*) have different growth strategies. Upper leaves of a *G. hirsutum* canopy are diaheliotropic, tracking the sun particularly in the early morning and late evening, increasing PFD to the upper leaves during these times relative to leaves of *G. barbadense* that display no heliotropism (Lang, 1973; Ehleringer and Hammond, 1987). This difference in leaf heliotropism was suggested to be beneficial to net canopy photosynthesis early in the season, but detrimental to photosynthesis due to a decreased distribution of PAR to lower canopy layers as leaf area index (LAI) increased (Fukai and Loomis, 1976).

In this study, photon flux incident to leaf surfaces and penetration within the canopy were determined for *G. hirsutum* and *G. barbadense*. In addition to distinct heliotropic responses, *G. hirsutum* and *G. barbadense* had unique canopy architectures due to variations in development of leaf area and leaf shape as determined by the degree of folding or cupping of the leaves. *G. barbadense* leaves were much more folded than *G. hirsutum*, and this leaf developmental strategy was accentuated over the course of the growing season. Additional differences in placement of leaves and leaf sizes resulted in distinct canopy architectures for the two cotton species. The impact of these two growth strategies on light environment within the crop canopies was determined by measuring the photon flux distribution within the canopies.

2. Material and methods

2.1. Plant growth

Cotton seeds (*G. hirsutum*, cv. Delta & Pine Land 5415, and *G. barbadense* cv. S-6) were planted in a well drained sandy loam in 1 m rows in 12 by 12 m plots at Mississippi State on May 19, 1993 using a Kenze dual-frame no-till cotton planter. Plants were thinned by hand to approximately 10 plants per m row. Nitrogen was applied at 5.6 $g\,m^{-2}$ at planting, followed by 4.5 $g\,m^{-2}$ at lay-by. Potassium was broadcast 35 days prior to planting at the rate of 6.7 $g\,m^{-2}$. Standard agricultural practices were followed for weed and insect control. Measurements of leaf and canopy structure and PAR profile were taken prior to canopy closure (43 days after planting (DAP)), and after canopy closure (74 DAP). At 43 DAP the plants typically had 8 fully expanded mainstem leaves, while at 74 DAP there were 18–20 mainstem leaves.

2.2. Measurement of leaf and canopy structure

Non-destructive determinations of LAI within the canopy were made using a LiCor LAI 2000 plant canopy analyzer [1] (Welles and Norman, 1991). Non-destructive LAI measurements were made only after canopy closure due to the large gaps between rows and small plant size early in the season. LAI at different heights within the canopies was determined by leveling the LAI 2000 sensor on a support at a known height within the canopy. A 270° view field was used, and a minimum of five separate readings were taken along a diagonal transect in the row as described (LiCor, 1992). Three different rows were measured for a total of 15 separate measurements at each canopy height for each plot. All measurements with the LAI 2000 were made under diffuse skylight conditions at dawn or dusk, as recommended for accurate determination of leaf area index (LiCor, 1992). Following non-destructive measurements of LAI, destructive harvests of leaves were made at different plant heights. Both leaf area and leaf shadow were measured using an image analyzer system (Ikegami area meter, Ikegami Tsushinki Co. Ltd., Utsunomiya, Japan). The 'shadow' of the leaf in its natural configuration was measured as the projected two-dimensional area when the leaf was illuminated from above with a light source perpendicular to the plane of the leaf midrib. After measurement of the leaf shadow, the leaf was flattened and the total leaf area measured. All leaves within one meter of row were measured for determination of LAI. Only leaves that were fully mature were used for determination of the ratio of leaf area to leaf shadow.

2.3. Determination of canopy light profile

Prior to canopy closure (43 DAP) and again after full canopy development (74 DAP), light profiles within the canopies were determined. Gallium arsenide phosphide photodiodes (GaAsP) were placed directly on the leaves to record incident PFD to the leaf surfaces (Gutschick et al., 1985). The small size and light weight of these sensors made them ideal to measure PFD to leaf surfaces in the photosynthetically active range from 400–700 nm while allowing freedom of leaf movement within the canopy. With the small 1.7 mm^2 active sensor area, the GaAsP sensors had the advantage of avoiding spatial averaging within one area of the canopy while allowing multiple measurements (Gutschick et al., 1985). The additional advantage of placing sensors directly on leaf

[1] The USDA neither guarantees nor warrants the standard of the product or service, and the use of the name USDA implies no approval of the product or service to the exclusion of others that may be suitable.

surfaces was the determination of light to receptive areas within the canopy and avoidance of gaps or clumps due to irregular distribution of leaves within a row, or row orientation (Fukai and Loomis, 1976; Gutschick et al., 1985). The spectral response curve of the GaAsP sensors was a good estimate within the range of photosynthetically active radiation (Pearcy, 1991). Shunt resistors were used to linearize the voltage output of PFD up to full sunlight. The individual calibration factors for each GaAsP sensor were determined by calibrating against a LiCor quantum sensor. Fine wires (leaf flutter leads) were used to attach the photodiodes to larger wires in order to allow maximum leaf movement (Roden and Pearcy, 1993). A section of canopy near the middle of each plot was chosen for placement of sensors in order to avoid edge effects. Given the regular development of leaves and the rate of leaf formation of cotton leaves, sensors were distributed evenly around the plant and at different heights within the canopy. Care was taken to avoid placement of sensors directly overhead others or clumping of sensors in one area of the canopy, giving a measure of PFD that was a representative average within the canopy. Depending on the age of the canopy, 10 to 24 sensors were used to determine PFD incident to the leaf surfaces. The sensors were connected through multiplexers to a datalogger system that recorded PFD every 10 seconds and calculated 1 min averages for each sensor individually over the course of the day. Incident PFD was determined as the sum of the PFD to each leaf over the course of the day. Total incoming solar radiation in the photosynthetically active range was measured using a LiCor quantum sensor placed 2 m above the canopy. All measurements were repeated for three days at the two intervals (43 and 74 DAP) during the growing season.

The measured incident PFD were corrected for changes in solar angle (Anderson, 1971; Jones, 1992). Photon flux levels recorded by leaf sensors were not corrected for solar angle, as the parameter of interest was the PFD incident to the leaf surface. Additionally, the extreme cupping of the *G. barbadense* leaves resulted in only a small fraction of any given leaf surface being oriented at one particular angle. The placement of sensors on non-horizontal leaf surfaces would result in less than a 15% error in calculated extinction coefficients, provided the leaf surfaces varied less than 45° from horizontal. The closer the leaf orientation angles were to horizontal, the smaller would be the error in calculated extinction coefficients. The average leaf orientation angles for *G. hirsutum* were 24.1° ± 2.5 and for *G. barbadense* were 29.4° ± 2.09, resulting in less than a 5% error in the extinction coefficients arising from the non-horizontal placement of PFD sensors on leaf surfaces. The extinction coefficient, k, was calculated as:

$$k = \frac{-\ln(I/I_o)}{L} \tag{1}$$

where I_o was the incident light; I was the light at the leaf surface; and L was the cumulative leaf area index through which the light passed (Jones, 1992). Extinction coefficients for the canopies were determined near solar noon, when differences in leaf angle due to solar tracking would be minimal. Each individual 1 min PFD reading was used to determine the attenuation of PAR within the canopy. Individual extinction coefficients for each leaf were averaged to determine the canopy extinction coefficient. Canopy extinction coefficients and cumulative LAI were corrected for changes in solar angle to determine canopy extinction coefficients at different times during the day (Sampson and Smith, 1993).

3. Results

3.1. Leaf structure

The leaves of *G. barbadense* have 3 to 5 lobes varying in size from the largest lobe along the midrib to small and often insignificant lobes at the outer edges. The shape of the individual lobes of the upper leaves are hemi-ellipsoidal, graduated in width and depth towards the tip of the lobe. The depth of the half-ellipse is often larger than the width at the innermost edge, creating a deep cupping of the leaves. The depth, a measure of the degree of curvature of the leaves, decreases at lower positions on the plant. Leaves of *G. hirsutum* have a similar overall leaf shape, but the individual lobes are not folded, but rather flatten rapidly.

Differences in leaf shape between the two species were determined by measuring the projected leaf area of all fully unfolded leaves in their natural three-dimensional shape and the total leaf area of the leaves after flattening. In the mature canopy, the area of the shadow cast by the upper mature leaves of *G. barbadense* was half of the total leaf area (Fig. 1). The extreme cupping of the *G. barbadense* leaves resulted in a leaf shadow that was slightly less than the shadow cast by mature leaves of *G. hirsutum*, even though the total leaf area of the *G. barbadense* leaves was significantly greater than the *G.*

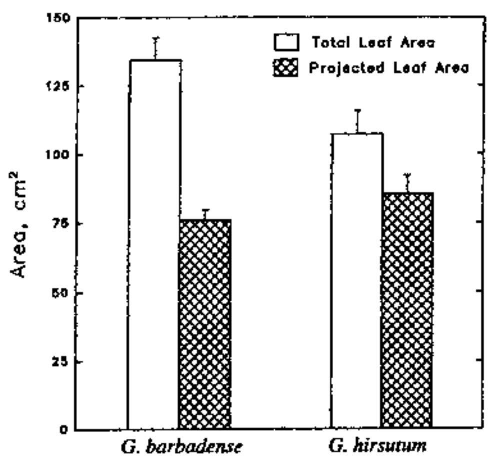

Fig. 1. Comparison of total leaf area to projected leaf area in mature upper canopy leaves. The total leaf area (open bar) and projected leaf area (cross-hatched bar) were determined for fully expanded leaves in the upper canopies of *G. barbadense* and *G. hirsutum*. Projected leaf areas were measured as the shadow cast by the leaf in its normal three-dimensional configuration using an image analyzer system. The leaves were then flattened and total leaf area was determined. Data + s.e. from a minimum of 10 mature leaves from the upper portion of each canopy is presented.

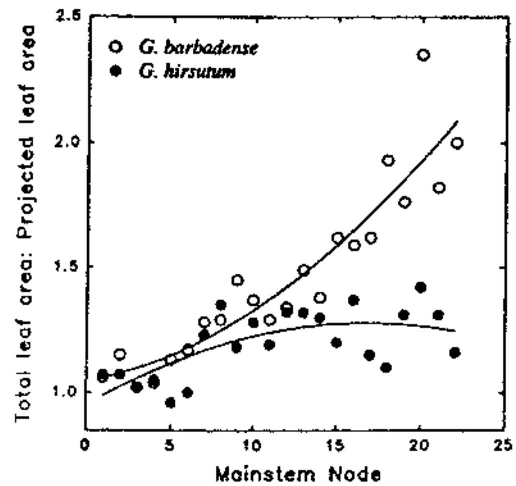

Fig. 2. Ratio of total to projected leaf areas. Total and projected leaf areas were determined for mainstem leaves of *G. barbadense* and *G. hirsutum* as described in Fig. 1. Only fully expanded mainstem leaves of *G. barbadense* (○) and *G. hirsutum* (●) are presented, though branch leaves displayed the same changes in three-dimensional structure with position.

hirsutum leaves. In the early part of the growing season (node < 10), the ratio of total to projected leaf areas was near unity for both species (Fig. 2). There was some cupping of the *G. hirsutum* leaves, resulting in a slight increase in ratio of total to projected leaf area over the course of the growing season. Conversely, as the *G. barbadense* grew, the leaves became progressively more cupped, increasing the degree of folding and hence decreasing the shadow cast by the leaves. This increased cupping resulted in an increase in the ratio between the total and projected leaf area over the course of the growing season.

3.2. Leaf photon flux distribution

The PFD incident to the leaf surface at any given time during the day equals the incoming PFD times the cosine of the angle of incidence. As described by Herbert (1983), the cosine of the angle of incidence for a leaf surface is dependent on four angles that describe the position of the leaf and the sun at any given time.

$$\cos\Theta = (\cos\alpha\sin\beta\sin\zeta + \cos\beta\cos\zeta)\cos\tau - \sin\zeta\sin\alpha\sin\tau \tag{2}$$

where α is the azimuth angle, given by the difference in compass direction between the leaf midrib and sun, ζ is the solar zenith angle, β is the elevation of the leaf midrib above horizontal, and τ is the angle of rotation or tilt of the leaf with respect to the horizontal (Herbert, 1983). For a leaf oriented due south (azimuth angle = 90°), and leaf orientation angle (β) at 0, Eq. 2 reduces to:

$$\cos\Theta = \cos\zeta\cos\tau - \sin\zeta\sin\tau \tag{3}$$

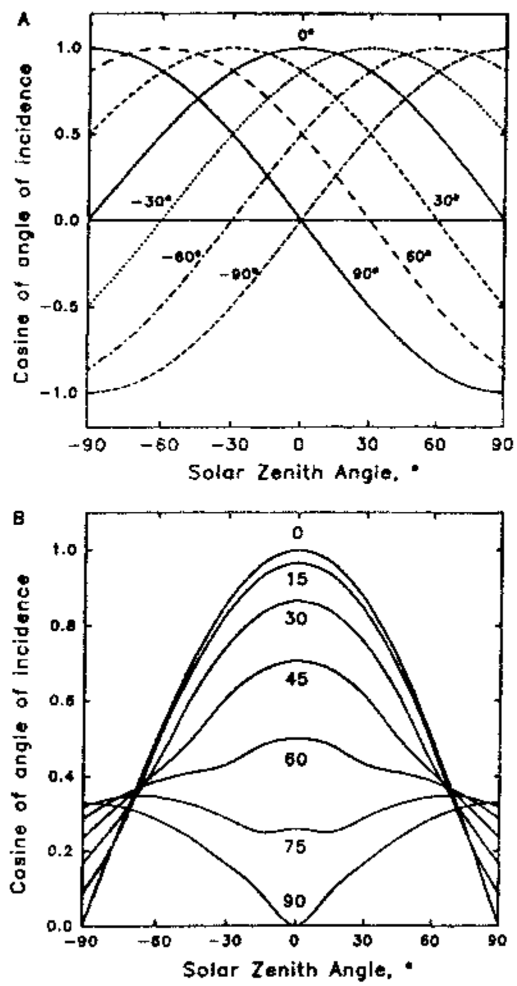

Fig. 3. Cosine of the angle of incidence for *G. barbadense* leaf surfaces. The change in the cosine of incidence angle for tangents to the cupped leaf surface for portions of a *G. barbadense* leaf with angle of rotation about the horizontal midrib (τ) changing from 90° (facing east) to $-90°$ (facing west) in 30° increments determined from Eq. 2 is plotted for the change in solar angle from sunrise ($-90°$) to sunset (90°). Leaf elevation angle (β) was held horizontal. (A) The cosine of incidence angle for a single leaf lobe with azimuth angle α between midrib and solar path = 90°. (B) The cosine of incidence angle for a *G. barbadense* leaf surface with angle of rotation τ ranging from 90° to 0° in 15° increments averaged over 180° change in α.

In the case of the hemi-ellipsoid of *G. barbadense* leaf lobes, τ is the angle above horizontal of the tangent to the hemi-ellipse at any given point along the leaf surface. The angle of the tangent will vary from zero at the midrib to near 90° at the leaf edges. The cosine of the angle of incidence will then vary over the course of the day, depending on the position along the ellipsoid (Fig. 3). At sunrise (solar zenith angle = $-90°$), the leaf surface facing east ($\tau = 90°$) has a cosine near 1, receiving near-full sun.

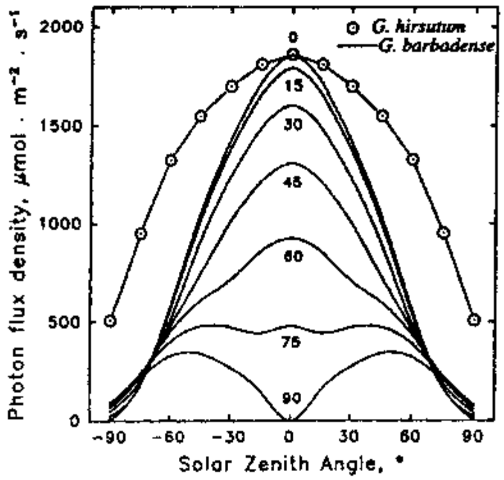

Fig. 4. Photon flux distribution across leaf surfaces. The average photon flux level across the surface of the main lobe of cotton leaves was determined from a diurnal light curve and the cosine of the angle of incidence (Fig. 3(B)). For *G. barbadense*, different sections of the leaf with rotation angle τ varying from horizontal (0°) to vertical (±90°) are determined in 15° increments along the leaf surface.

Conversely, the west-facing leaf surface receives near-full sun at sunset (solar zenith angle = 90°). The portion of the leaf receiving near-full sun changes over the course of the day as the solar angle changes. The region of the curves (Fig. 3(A)) below zero indicate that portion of the day during which the upper leaf surface is shaded and the abaxial surface is sunlit. Although the contribution to total carbon uptake within the canopy by illumination of the abaxial leaf surface may potentially be significant, as discussed below, the remainder of this discussion considers only illumination of the adaxial leaf surface. The cosine of the angle of incidence for tracking leaves, such as the much flatter *G. hirsutum* leaves, will remain near 1 throughout the day, as leaf rotation (τ) and orientation (β) angles adjust to match the change in leaf solar angle (ζ) (Ehleringer and Hammond, 1987).

Holding leaf inclination angle (β) horizontal, the cosine of the angle of incidence for portions of the *G. barbadense* leaf at different angles of rotations (τ) averaged over 180° rotation of α is presented in Fig. 3(B). The outermost edges of the cupped leaf receive the most direct sunlight early morning and late evening, while portions of the leaf surface at gradually lower positions along the ellipse receive more direct light closer to noon. The leaf surface near the midrib has the highest cosine of incidence angle at solar noon.

The average PAR levels at different positions along the hemi-ellipsoid of a *G. barbadense* leaf (Fig. 4) were determined from a typical diurnal PAR curve and the cosine of incidence angle (Fig. 3(B)). The cupped shape of the *G. barbadense* leaves resulted in different portions of an individual leaf receiving different amounts of PAR. The portions of the leaf with greatest τ values contributed little to the overall PAR absorbed by the leaf, while the portions of the leaf surface closest to the midrib

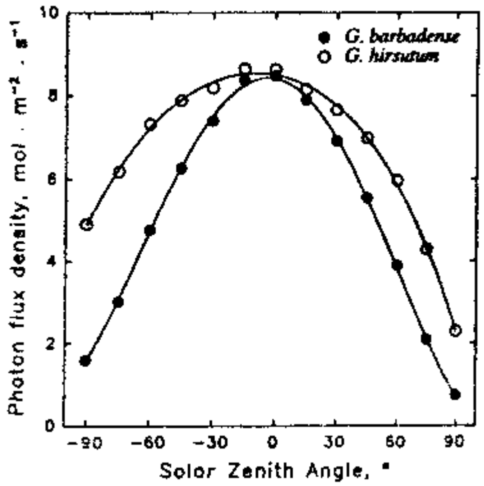

Fig. 5. Total photon flux across leaf surfaces. Comparison of the estimated PFD received by a typical leaf surface in the upper canopy of *G. hirsutum* and *G. barbadense*. The estimate is calculated from measured PFD values and derived cosine of incidence angle (Fig. 3(B)), taking into account differences in leaf area per unit ground area (Fig. 1), summed over the entire leaf surface.

contributed more, as they received more sunlight near solar noon. The *G. hirsutum* leaf, which adjusted leaf rotation and elevation angles to compensate for changes in solar zenith angle, received a greater average photon flux to the leaf surface over the course of the day.

Even taking into account the larger leaf area of a *G. barbadense* leaf relative to that of *G. hirsutum*, the total PAR received per m^2 of ground area was still significantly less than for *G. hirsutum*, except near solar noon (Fig. 5). From measured values of light incident to leaf surfaces, the estimated daily interception of uppermost leaves in the canopy was approximately 87 $mol\,m^{-2}\,day^{-1}$ for *G. hirsutum*, compared to only 67 $mol\,m^{-2}\,day^{-1}$ for *G. barbadense*.

3.3. Canopy structure

The distribution of leaves within canopies of *G. hirsutum* and *G. barbadense* was determined in destructive harvests of leaf material at two stages of canopy development, early season prior to canopy closure (43 days after planting) and after canopy closure (74 days after planting). The two cotton species showed differences in distribution of leaf area within the canopy at both stages of development, with *G. barbadense* having more leaf area particularly in the mid-range of the canopy (Fig. 6). This difference was particularly evident after canopy closure.

The leaf area index was measured using both destructive and non-destructive sampling methods. Early season plants were too small to allow accurate determination of LAI using the non-destructive sampling method, therefore plants were only sampled destructively. The early season canopies showed very little difference in LAI between

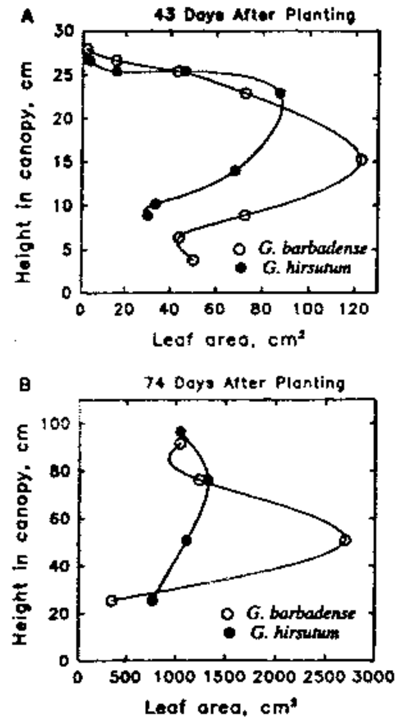

Fig. 6. Distribution of leaf area within plant canopies. Leaf areas were determined in destructive harvests of leaves as a function of height within the canopy for *G. barbadense* (○) and *G. hirsutum* (●). All plants in 1 m of row were sampled prior to canopy closure (43 days after planting) and after canopy closure (74 days after planting). Total leaf area was measured on the flattened leaves using an image analyzer system.

the two species (Fig. 7(A)). After canopy closure, however, the *G. barbadense* canopy had a greater LAI as determined from the destructive samples, reaching a final LAI near 6 (Fig. 7(B)). Interestingly, the LAI determined by the LAI 2000 gave a nearly identical distribution of leaf area within the two mature canopies (Fig. 7(C)). The LAI at ground level was slightly less for the *G. hirsutum* canopy from that measured in the destructive samples, and significantly less for the *G. barbadense* canopy.

3.4. Canopy light environment

The diurnal photon flux throughout the canopy was determined using small gallium arsenide phosphide photodiodes placed directly on the leaves, which have the advantage of measuring the PFD incident to the individual leaf surfaces. The diurnal PAR levels measured for each leaf were integrated to determine the total daily photon flux received by the individual leaves.

Prior to canopy closure, there was a rapid attenuation of PAR within both canopies (Fig. 8). This decrease in PFD with increasing LAI in the immature canopy was greater for *G. barbadense* than *G. hirsutum*. Early in the growing season, PAR attenuation was

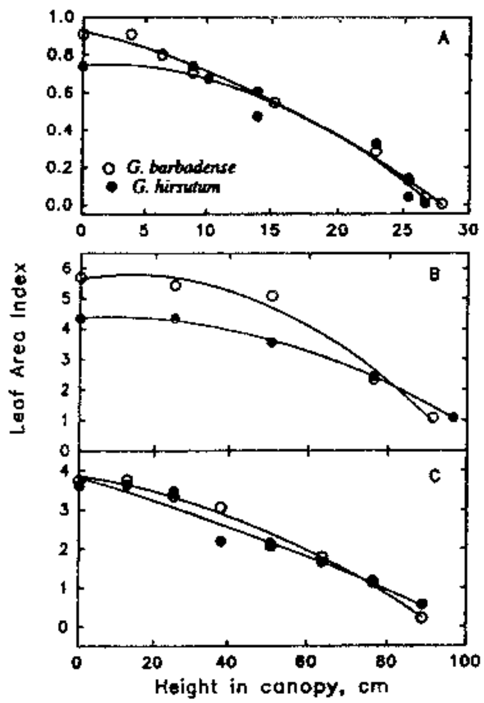

Fig. 7. Leaf area index. Leaf area index was determined from total leaf area at different canopy heights as described in Fig. 6 for *G. barbadense* (O) and *G. hirsutum* (●). (A) LAI determined from total leaf area with plant height prior to canopy closure (43 DAP) using destructive leaf sampling method. (B) LAI determined from total leaf area with plant height after canopy closure (74 DAP) using destructive leaf sampling method. (C) LAI determined after canopy closure using non- destructive method (LAI 2000 Plant Canopy Analyzer).

more rapid in the *G. barbadense* canopy than in the *G. hirsutum* canopy. The rapid attenuation of PAR relaxed over the course of the growing season, becoming less in the mature canopy (Fig. 8). The mature canopy of *G. barbadense* displayed a more gradual decrease in photon flux with LAI than that of *G. hirsutum*, resulting in a greater PFD reaching the lower leaves of *G. barbadense*. The decrease in PFD at lower canopy heights was particularly striking in the *G. hirsutum* canopy, as leaves below mid-height in the canopy received very low PFD on a diurnal basis. In contrast, the *G. hirsutum* leaves near the top of the canopy received photon flux levels that were near full sun, whereas those of *G. barbadense* did not.

Light penetration within the canopies was determined using the extinction coefficients calculated with Eq. 1. The early season canopy was best fit with the Markov model (Nilson, 1971):

$$a(L,r_s) = e^{(-k\lambda L)} \tag{4}$$

where $a(L,r_s)$ was the fraction of sunlight, k was the extinction coefficient, L was cumulative leaf area index, and the variable λ indicated the leaf distribution. Canopy PAR profiles were determined by averaging the measured PFD incident to leaves in

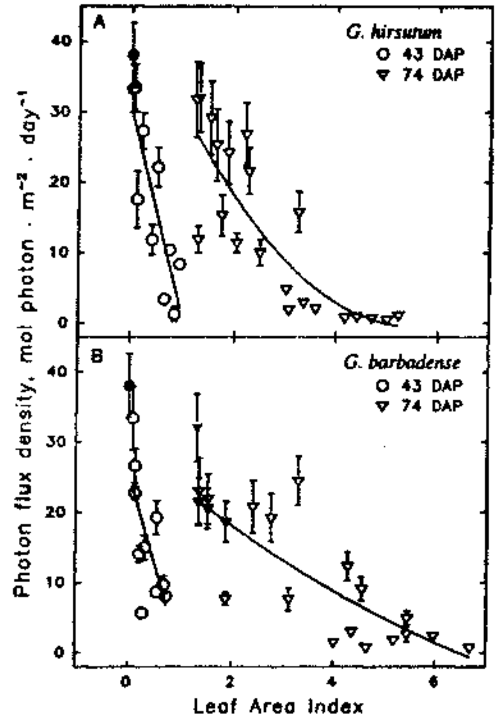

Fig. 8. Attenuation of light as a function of leaf area index. Total diurnal light received by leaves of a single plant within a *G. hirsutum* (A) and *G. barbadense* (B) canopy was determined from the sum of the diurnal PAR measured by gallium arsenide phosphide photodiodes and presented as a function of leaf area index within the canopy. Measurements were made prior to canopy closure (○) and after canopy closure (▽) and repeated over three days at each of the time periods. The total daily insolation received over the three day periods for early (●) and mid season (▼) are shown.

hourly increments over the course of the day for the 3-day measurement period. Photon flux profiles at early morning (1 h after sunrise) and midday (at solar noon) were compared (Fig. 9). The early season *G. hirsutum* canopy (43 DAP) showed a clumped distribution. Light penetration was similar at both early morning ($\lambda = 0.8$) and midday ($\lambda = 0.9$). The early season *G. barbadense* canopy had a regular distribution at midday ($\lambda = 1.3$), with a sharp linear drop in PFD in the early morning. Notably, the upper leaves of *G. barbadense* received very low PFD in the early morning, and PAR attenuation within the canopy at midday was more rapid than for *G. hirsutum*.

The closed canopy (74 DAP) showed a regular distribution early in the morning for both *G. hirsutum* ($\lambda = 1.7$) and *G. barbadense* ($\lambda = 1.3$) (Fig. 10). As with the early season canopy, upper leaves of *G. barbadense* received very little light in the early morning. The midday closed canopies both showed a random distribution ($\lambda = 1.0$), and so the radiative transfer model of Fukai and Loomis (1976) was used to describe the light attenuation (Fig. 10). In this model, the light penetration was described by:

$$a(L,r_t) = (1 - Sk)^{L/S} \tag{5}$$

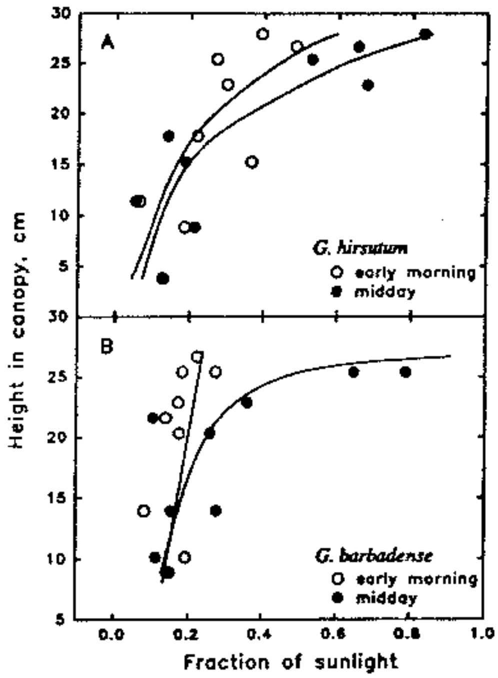

Fig. 9. Radiative transfer within early season cotton canopies. Penetration of light within the early season canopy (43 DAP) was described using a Markov model (Eq. 4) (Nilson, 1971). Incident PFD was averaged in 1 h increments in early morning (1 h after sunrise) and midday (solar noon) for the 3-day measurement period. *G. hirsutum* showed a similar clumped distribution early morning ($\lambda = 0.8$) and midday ($\lambda = 0.9$). Photon flux distribution within the *G. barbadense* canopy early morning showed a linear decrease, while midday showed a regular distribution ($\lambda = 1.3$).

where $a(L, r_s)$ was the fraction of sunlight, k was the extinction coefficient determined from Eq. 1, L was the cumulative leaf area index, and S was the ratio of the area of an individual leaf to the ground area over which it is considered to exist (Fukai and Loomis, 1976). The best fit to the data gave a value of $S = 0.7$ for the mature *G. hirsutum* canopy at midday (Fig. 10(A)). The upper half of the *G. barbadense* canopy was best fit by $S = 0.1$, while the lower half was best fit when $S = 0.3$ (Fig. 10(B)). In a reversal of the early season pattern of PAR penetration within the midday canopies, PAR attenuation in the closed canopies was more rapid in the *G. hirsutum* canopy than in the *G. barbadense* canopy.

4. Discussion

Optimization of crop structures indicate that more vertical placement of upper canopy leaves increases net canopy photosynthesis due to decreased PFD to already light-saturated upper leaves and redistribution of PAR to light-limited lower canopy leaves

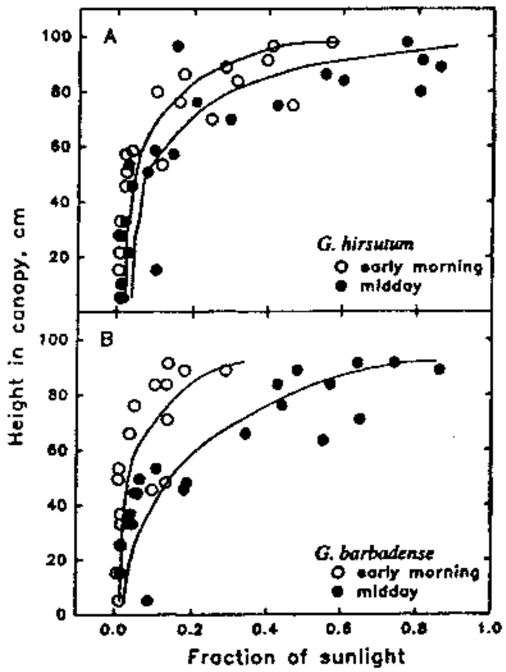

Fig. 10. Radiative transfer within closed cotton canopies. Photon flux density after canopy closure (74 DAP) showed a regular distribution in the early morning for both *G. hirsutum* ($\lambda = 1.7$) and *G. barbadense* ($\lambda = 1.3$). The radiative transfer model of Fukai and Loomis (1976) (Eq. 5) was used to describe the PAR penetration within the mature closed cotton canopies at midday. Photon flux within the *G. hirsutum* canopy was fit to the model with $s = 0.7$. Photon flux within the *G. barbadense* canopy was best fit to the model using $s = 0.1$ for the upper half of the canopy (> 50 cm), and $s = 0.3$ for the lower half of the canopy (< 50 cm).

(Herbert, 1991; Herbert, 1992). Kuroiwa (1970) found increased photosynthetic activity in model canopies having leaf inclination angles that changed from 90° for the upper canopy leaves to 0° for the lower canopy leaves.

The two agriculturally significant species of *Gossypium* display different strategies of growth and interception of incident PFD, as seen in the different shapes of the leaves and the different heliotropic responses. *G. barbadense* had large, fairly flat leaves early in the season that progressively became more cupped (Fig. 2). This increased leaf cupping at higher canopy positions was not the result of leaf age, but rather an alteration in the type of leaves that developed at different stages of crop growth. This cupping resulted in a leaf surface area that was twice the leaf shadow area (Fig. 1). The large degree of cupping in upper *G. barbadense* leaves resulted in an uneven distribution of PAR over the surface of the leaf (Fig. 4), and significantly reduced the total PAR incident to the upper canopy leaf surfaces (Fig. 5). Different portions of the leaf surface received full-sun at different times of the day (Fig. 3), with no one section of the leaf remaining near full-sun for any extended period of time.

The second factor that reduced photon flux to upper canopy leaves of *G. barbadense* was the lack of solar tracking. This was particularly evident in the early morning light profiles in both early and closed canopies (Figs. 9 and 10). In comparison to the diaheliotropic *G. hirsutum* leaves, the *G. barbadense* upper canopy leaves received significantly less PAR over the course of the day (Fig. 8). The PAR penetration into the canopy was not significantly altered by the lack of solar tracking, as both *G. hirsutum* and *G. barbadense* displayed a rapid attenuation of PAR within the canopies in the early morning (Figs. 9 and 10). Additionally, the greater PAR penetration to lower layers in *G. barbadense* at midday compared to *G. hirsutum* after canopy closure could not be attributed to differences in solar tracking, as adjustments in leaf inclination and elevation angles would be minimal near solar noon. Rather, the cupping of the upper canopy leaves of *G. barbadense* resulted in a more erectophile canopy, and this allowed a greater penetration of PAR to lower canopy leaves. Thus, although the individual leaf inclination angles of *G. barbadense* did not change with position in the canopy, the inclination of the leaf surface approached 90° due to cupping of the leaf sides, resulting in an overall canopy structure of *G. barbadense* that mimicked the theoretical optimal canopy described by Kuroiwa (1970). The gradual increase in leaf cupping in the *G. barbadense* canopy (Fig. 2), while reducing photon flux to upper canopy leaves (Fig. 5), distributed the available PAR over a greater photosynthetically active leaf area in the upper canopy (Fig. 1), albeit at a lower average light intensity (Fig. 4). The cupping of the *G. barbadense* leaves resulted in a greater leaf area per unit ground area (Fig. 7), increasing the photosynthetically active area, and simultaneously dispersed the incoming PAR to lower areas of the *G. barbadense* canopy where a greater proportion of the leaf area was located (Fig. 6(B)). Thus, alteration of leaf rotation angle (τ) by cupping of the leaf surface about the midrib appears to be a viable method of altering leaf and canopy PAR distribution.

Knowledge of total leaf area is physiologically important in order to determine the total potential photosynthetically active area. The projected leaf area is physically important in order to define the canopy structure, since the area of leaves that intercepts PAR determines the attenuation of PAR within the canopy. To this end, different measures of LAI may be necessary to accurately determine total leaf area or projected leaf area. For a canopy composed of somewhat regularly shaped leaves, the non-destructive measurement of LAI using the LAI 2000 plant canopy analyzer is accurate (cf. Fig. 7(B),(C); Welles and Norman, 1991). However, for leaves with a large folding of the leaf shape, this method underestimates total LAI (Fig. 7), as has been previously described (Grantz et al., 1993). Chen and Black (1992) suggested that for highly folded leaves, a better estimate of the projected leaf area should be based on half of the total single-sided leaf area measured. In the destructive determination of total LAI, the LAI at ground level in the *G. barbadense* canopy reached nearly 6, while that in the *G. hirsutum* canopy was just above 4 (Fig. 7(B)). Leaf area index with plant height measured with the LAI 2000 Plant canopy analyzer, which sees the projected and not the total leaf area, was lower and nearly identical for both species, as may be expected from the similarity of projected leaf areas measured for the two species (Fig. 1). Inclusion of portions of the abaxial leaf surfaces as viable contributors to overall canopy carbon uptake would further increase the overall photosynthetically active leaf surface area in *G. barbadense*.

The cupping of upper canopy leaves of *G. barbadense* results in more PAR at a lower intensity to a greater leaf surface in the upper portion of the canopy, and more PAR penetration to lower canopy layers. In addition to distributing more PAR to lower layers, this strategy may be advantageous by reducing photoinhibition to upper canopy leaves by reducing the time and intensity of PAR exposure (Figs. 3 and 4). However, the efficacy of distributing more PAR to older leaves lower in the canopy is unclear, since particularly in cotton, leaves rapidly lose photosynthetic capacity with aging (Wullschleger and Oosterhuis, 1990). In addition, the degree of cupping in *G. barbadense* is commonly so extreme that the abaxial leaf surface is oftentimes in full sun. Measurements of vertically restrained *E. maculata* leaves indicates a near-equal photosynthetic potential when either abaxial or adaxial leaf surface is illuminated (Evans et al., 1993). Development of the photosynthetic apparatus and leaf anatomy is dependent on the PAR environment during development (Terashima et al., 1986), though the physiological response of leaves can adapt to changes in PAR environment (Ögren and Evans, 1993). Studies in cotton have determined a difference in light response between abaxial and adaxial stomata (Nagarajah, 1975; Lu et al., 1993), though no studies have examined the anatomical or physiological differences in the near-vertical sections of *G. barbadense* leaves. The significant portion of abaxial surface sunlit, albeit at low early morning and late evening photon flux levels (Fig. 3(A), suggest that photosynthetic activity of the abaxial leaf surface may contribute significantly to the overall canopy canbon uptake, and may be another possible benefit of the extreme leaf cupping of *G. barbadense*.

Although the total diurnal PAR interception is important in determining the potential carbon uptake by a particular leaf, the distribution of the PAR is critical to determining the readiness of that leaf to utilize the incoming PFD (Pearcy, 1990). The typically rapid fluctuations in sunlight over the course of the day affect the photosynthetic activity by altering the activation states of enzymes involved in carbon fixation (Sassenrath-Cole and Pearcy, 1994). A minimum PFD is necessary to maintain these enzymes in an active and competent state in order to fully utilize the rapid photon flux transients. The growth strategy of the *G. barbadense* leaves maintains a greater PFD to lower canopy leaves, potentially increasing their contribution to total carbon uptake. Additionally, elevated PFD to lower canopy layers have been suggested to be important in fruit development in cotton (Constable, 1986).

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